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MELANIC TENDENCIES IN PHALAENID AND GEOMETRID MOTHS IN EASTERN PENNSYLVANIA

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Although Industrial Melanism has come to be a standard citation in the literature of genetics and evolution, relatively little has appeared in the United States on the subject. Few descriptions of melanics on this side of the Atlantic have found their way into print, nor have the few that have been remarked received much attention from the geneticists. This paper gives records of 15 species showing melanic tendencies in Pennsylvania, with frequency data for the commoner forms; several of these species have not been reported previously as having melanic forms. The evolutionary implications of the melanism are discussed following the enumeration of species.

GEOMETRIDAE

Several of the classic Palaearctic mutant melanics occur in this family, especially in the tribe Cleorini of the Ennominae, and the best-known of the American ones, namely *Amphidasys cognataria* Gue. and *Phigalia titea* Cram., are congeneric with Old World species having melanic forms (*A. betularia* L. and *P. pedaria* Fabr.). In *A. cognataria* the black form[1] (which is solidly black, without markings) is decidedly more frequent than the "normal" in eastern Pennsylvania. The species is very common and data are available for a number of localities, but too little is known of the movements of individuals and the characteristics of the population of this, as of most nocturnal moths, for a really meaningful analysis to be made of the variation in frequency of the melanic form noted from different (urban vs. rural) sampling stations. The over-all frequency of the melanic phenotype appears to be 60-65% of both sexes.

In the very abundant spring species, *P. titea,* the melanic form is less frequent than the "normal", but a marked rise in frequency has been observed in recent years in Pennsylvania. The increase was especially notable in March-April, 1963, in which season the species was also unusually abundant in general. As pointed out by Ford and others, unusual abundance of a species is as a rule accompanied by extraordinarily wide latitude in variation, and this was the case here. While the number of

total melanics exceeded 25% of the males for the first time at nearly all sampling stations, several partial melanics of previously unknown types also appeared. The usual melanic form as in *cognataria*, is solid black. The partial melanics were of two types: either black, with the submarginal band on all wings normal gray; or dark, uniform charcoal-gray, with the darker markings indistinctly visible above and beneath. Examples of all of these types are in the collection of the author. The frequency of total melanics in 1959-61 was 10-15%, and in 1962, ca. 18%.

Melanism occurs in a large number of Cleorini in Pennsylvania. Aside from these two common, well-known species, several of the less common forms have shown melanic tendencies. The distinctive *Epimecis virginaria* Cram. has developed both partial and complete melanism. The partial melanics are dark, brownish-gray, with the three principal lines of the wings unsuffused over their light edging (basad on the postbasal line, and marginad on the median and submarginal ones). The total melanic is solid black with the exception of these same three light lines, which are even more conspicuous on the black ground.[2] *E. virginiaria* is uncommon at the latitude of Philadelphia and northward, but the black form seems to be occurring with considerable frequency, the combined values of the two dark types probably reaching at least 50% (of which at least 35% is "total"). One melanic specimen of *Paraphia subatomaria* Wood has been taken in Chestnut Hill, Philadelphia (28 July 1962); it and the related *P. unipuncta* Haw, are both uncommon to rare.

Another related species with melanic tendencies is the scarce *Nacophora quernaria* Ab. & Sm. This insect is too uncommon for any reliable frequency figure to be available for the melanic form in eastern Pennsylvania. Less than a dozen area specimens have been seen by the writer. The melanics[3] have the ground-color full black, with the white edging of the postbasal and postmedian lines (basad and marginad, respectively) conspicuously unsuffused. No melanics have yet turned up in the rare spring species, *Lycia ursaria* Walk., but they may be expected.

Two more possible instances are found in the Cleorini, namely *Cleora pampinaria* Gue. and *Ectropis crepuscularia* L. Both of these common insects have a wide range of variation from very light to very dark gray forms. One fully black *pampinaria* was taken at Flourtown, Montgomery Co., Pa., 8 September 1963. A single melanic specimen of *crepuscularia* has been described.[4] The writer has not seen any black Pennsylvania individuals of this species.

The important pest, *Palaeacrita vernata* Peck, is quite variable in color, and a good case for melanism can be made when the

darkest forms are compared with the lightest. No fully black individuals have been taken, and the character is apparently not so clear-cut as in other Cleorines. The darkest individuals seem to be more frequent in recent years than previously, however.

One more indisputable case of melanism in the Geometridae concerns a member of the Sterrhinae, *Cosymbia lumenaria* Gue. Two black specimens were taken in 1963 (Flourtown, 7 July; Conshohocken, 11 Aug., both Montgomery Co.), both with the discal spots and the pastmedian line on all wings the usual pale gray, contrasting with the sooty ground-color. The species is rather uncommon in the area, and no frequency figure can really be given.

PHALAENIDAE

The best-known species with melanic tendencies in the Phalaenidae is *Charadra deridens* Gue. It is common and the frequency of the black forms in Pennsylvania is at least 50% and probably somewhat higher. Some of the melanics are solid black; most have the postmedian line white, and a few have the postbasal line white also. The second of these was described in 1923.[5] All have the normal black markings faintly discernible. A few females seem to be intermediate between the "normal" and melanic phases, being moderately suffused with black scales.[6] Two scarce species contribute additional records. *Panthea furcilla* Pack. has a nearly melanic form which is considerably darker than the typical form, but the dark markings remain visible. *Polia latex* Gue. has a black form, previously unrecorded, also with the dark markings still identifiable. Both are too uncommon for frequency figures to be available. Dark *furcilla* have been taken for several years in Philadelphia, and the first melanic *latex* was taken at Conshohocken, Montgomery Co., 11 May 1963. One more possible case of melanism is *Marasmalus inficita* Walk., but the citation rests on but a single melanic specimen (Norristown, Montgomery Co., 9 August 1961). The species is quite uncommon.

NOTODONTIDAE

Two Notodonts appear to have melanic forms, namely *Cerura cinerea* Walk. and *Lophodonta ferruginea* Pack. Both appear to have a relatively high frequency, although the second species is generally much commoner than the first, and hence more readily analyzable. In both, the melanism is quite noticeable, although in *cinerea* it is a dark charcoal gray, not a black, form. The frequency in *ferruginea* has been about 60% for several years, indicating that, as in *A. cognataria*, the darker has become the statistically "normal" form.

In 1927 Chermock described melanics of *Heterocampa umbrata* Walk.[7] and in 1929 of *Fentonia marthesia* Cram.,[8] both

from Pittsburgh. Both species occur in the writer's sampling area, but no melanics have been found of either. One black specimen of *Schizura apicalis* G. & R. has been taken (Flourtown, Montgomery Co., 14 June 1963). The species is uncommon. A possible second melanic of the same species, in very poor condition, was taken 8 July, 1959 (Norristown).

DISCUSSION

There seems to be adequate evidence to support the notion that melanism is fully as widespread in America as in Europe. Of particular interest is the regularity with which melanism occurs in species having a certain facies in the "normal" type condition, i.e. silvery-gray moths with black markings or dusting, irrespective of family. It becomes possible to predict the occurrence of melanics in various species; the writer actually did predict that melanic *Cleora* would be found, a year before the first specimen known to him turned up. In several cases where melanism has not appeared within a species where it might be expected on the basis of wild-type coloration, a black sibling species exists instead; for example, *Tolype velleda* Stoll and its dark sibling *laricis* Fitch (Lasiocampidae).

Many of these melanics seem to recur sporadically in widely separated localities. The evidence would suggest that the large number of apparently new melanics turned up by the author in recent years is not really unusual, but rather the result of more assiduous collecting. Many species which show melanism today have had melanic "aberrations" described in the past, mostly on the basis of single specimens, and the genetic continuity of some of these with present-day melanics in the same species is often dubious. The melanic form of *Phigalia titea* is perhaps the best documented, and seems to have arisen spontaneously in various parts of the range at various times, meeting with variable success in different localities. In at least some of the species concerned, the rate at which the mutation to "melanic" occurs must be fairly high. The more often a specific mutation occurs, the more likely it is that it will at one time or another occur in a situation or environment where it will be advantageous, or it least not deleterious. Under such circumstances it is likely to be preserved and propagated. It is specifically this fact that the orthogenecists have seized upon to support their inference of a "direction" or "purpose" in evolution. All we can say at present is that certain genes seem to show an instability (probably chemical), and that in the cases here considered, that instability leans in the direction of melanism.

Several of the lesser known of the examples cited have been found only quite recently, and in the absence of prior records it is impossible to state to what extent they have been present in the past, either genetically continuous with the current form or as a result of previous mutation of the same type. It is of some interest, however, to consider the future of any given melanic mutation which may be assumed to have just arisen *de novo*. Most "industrial" melanics whose genetics have been studied have proved to be unifactorial, autosomal dominants. This is true of at least *A. cognataria* in the U. S., as well. The selection against deleterious dominant mutations is most effective, so that for a dominant mutation to be successful it is not even enough for it to be adaptively neutral; it must have some adaptive advantage attached to it. What are the factors determining whether or not a given moth melanic will succeed biologically (be selected "for" or at least not selected "against")?

The conventional explanation of the development of "industrial melanism" in England was that the melanics had a concealment advantage in the industrial areas. This may be true under conditions of extreme contamination by soot, where the landscape is physically blackened, but it is of dubious value under other circumstances. It is true that in England at least, the highest percentages of melanics have been found to coincide with urban-industrial centers. This has led to an alternative explanation, namely, that the urban-industrial conditions have discouraged predators which would weed out the conspicuous melanics, and that in consequence the pressure of selection has been decreased, allowing the dominant melanics to spread. Further, several authors have reported that the melanics in several Palaearctic species possess a higher survival value under adverse conditions (e.g., semi-starvation) in the larval stage. This higher viability complements the second hypothesis nicely, in that it augments neutrality by giving an advantage which accounts for the rather steep frequency increases observed. This differential viability would be especially significant if it were to be demonstrated that the melanics are more resistant to urban-industrial atmospheric pollutants, such as SO_3.

It is difficult to state to what degree the melanism in American species is associated with urban-industrial conditions. As previously remarked, there are not sufficient data available for most species to support a meaningful and truly significant analysis. The two exceptions, *A. cognataria* and *P. titea*, so far as the

presently available Pennsylvania data would indicate, seem to follow the British trend of correlation well. Since the urban-industrial complex in question—Philadelphia and vicinity—is not characterized by extensive soot contamination, we may reasonably inquire into the means of maintenance of melanism thereabouts. The only concealment advantage for melanics which is apparent as a result of civilization there would be on asphalt highways; and it is rare indeed to find a moth of any kind resting horizontally on the ground. Most of the species having melanic forms rest by day on tree trunks, and several sit down among dense foliage in the ground-cover story. These facts suggest that of the three possibilities suggested for the maintenance of the melanism, concealment value may be the least significant. We do not, of course, know whether the pleiotropic increased viability exhibited by Cleorine melanics (at least in Europe) is shared by melanics in other species groups; it would be expected that the melanism in various families and subfamilies would have arisen by mutation of various non-homologous genes in somewhat different genetic systems; increased viability would not, then, be likely consequential generally. We do not know enough about moth biochemistry to state whether the viability increase is a direct result of the increase in melanin, or vice versa, or whether the two effects are interlocking but not in direct sequence (as where an enzyme may play a key role in two sets of concurrent reactions). Similar melanizing effects in different species may be produced in quite different ways, by different enzymes in different reaction sequences. The writer would like to see the progress along these lines coming, at last, from the laboratories of American researchers.

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3. *N. quernaria* "form *atrescens*" Hulst, Can. Ent. XXX (1898), p. 162.
4. *E. crepuscularia* "ab. *fumataria*" Minot, Proc. Bost. Soc. Nat. Hist. XIII (1869), p. 84.
5. *C. deridens* "form *fumosa*" Draudt, in Seitz, Macrolep., N.A. Noct. VII (1923), p. 19.
6. *C. deridens* "var. *nigrosuffusca*" Strand, Archives Naturgeschicter, A(2) (1917), p. 46.
7. *H. umbrata* "ab. *nigra*" Chermock, Bull. Brook. Ent. Soc., XXII (1927), p. 118.
8. *F. marthesia* "ab. *nigra*" Chermock, Bull. Brook. Ent. Soc., XXIV (1929), p. 20.